

Phanerotinus cristatus (Phillips) and the nature of euomphalacean gastropods

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Synopsis

New specimens of *Phanerotinus cristatus* (Phillips) found in the Lower Carboniferous of Cumbria have contributed to a re-appraisal of the morphological characters and function of this unique gastropod, which confirms that it belongs to the Euomphalacea. Various morphological features and the relationships of this superfamily are evaluated. A revised classification of the superfamily, eliminating some post-Palaeozoic genera, is proposed.

Introduction

Several factors have led to this paper on *Phanerotinus cristatus*. A certain uneasiness concerning the published interpretation of this unusual gastropod prompted one of us (N.J.M.) to re-examine the original material in order to establish how such an animal may have functioned. The comparative rarity of the species, which may have been limited to Britain and of which only three further specimens have been recognized in the 150 years since it was first collected, underlines its position as an object of interest. The historical background and involvement of a number of the important figures in nineteenth-century British palaeontology with the collection and description of the original specimens, in the Gilbertson collection, also provided a further motive, but it has now been decided to discuss this aspect elsewhere.

William Gilbertson (1789–1845), a pharmaceutical chemist in Preston, Lancashire, diligently amassed a unique collection of Palaeozoic fossils, mainly from the Carboniferous Limestone outcrops in the Clitheroe district of the neighbouring county of Yorkshire. Owing to the use of this collection by many of the earlier descriptive palaeontologists such as John Phillips (1836) and J. de C. Sowerby (1827–1844), see Cleevely (1974), Gilbertson could be regarded as the most significant and influential of the earlier collectors resident in the north of England. He may well have considered offering the collection to the British Museum while it was still in use by Sowerby, for correspondence in the Sowerby archive requests the return of borrowed specimens; soon after, in 1841, it was acquired by Dr J. E. Gray for the Dept. of Zoology, where it remained until transferred to the Dept. of Geology in 1881.

The early descriptions of the large, ornate, but rather rare genus *Phanerotinus* J. de C. Sowerby, 1844, from the Lower Carboniferous of Britain, were based on a single specimen in the Gilbertson collection. Yet these descriptions covered all the more important and distinctive characters of this unusual fossil gastropod: its large size, the regularly open-coiled shell and the very long sawtooth-like projections on its outer margin. Unfortunately, the natural breakage of the specimen had occurred along the relatively smooth base and a clear idea of the arrangement of these distinctive projections was difficult to obtain. In fact, both Phillips (1836) and Sowerby (1844) were led to suggest that there were two rows of such spines. However, the acquisition of a further specimen, from the Tennant collection in 1881, eventually contributed to a careful study by Knight (1941 : 239) which established that only a single row existed. He explained that flattening and consequent breakage during fossilization had led to the false impression that there were two rows of projections.

The fortunate discovery of two further specimens in the collections of the Institute of Geological Sciences has assisted in the re-appraisal of the genus. Closer examination of the Tennant specimen utilized by Knight has revealed that a small area of the dorsal surface of the shell is preserved and this clearly shows a re-entrant sinus at the top of the adapical margin. Sectioning of this same unique specimen has enabled us to discover further ornament detail. We have been able to reinterpret the nature of *Phanerotinus*, and confirm its status within the family Euomphalacea.

Taxonomic description

Superfamily EUOMPHALACEA de Koninck, 1881

Family EUOMPHALIDAE de Koninck, 1881

Genus *PHANEROTINUS* J. de C. Sowerby, 1843

TYPE SPECIES. *Euomphalus cristatus* Phillips (1836), by subsequent designation of de Koninck (1881 : 107).

REMARKS. Other species included in this genus by earlier authors, e.g. J. de C. Sowerby (1844) and Fischer (1885 : 852), belong elsewhere.

The genus *Elkoceras* Lintz & Lohr, 1958, misinterpreted as a cephalopod in its original description, is included as a synonym of *Phanerotinus* in the addendum of the Treatise (Knight *et al.* 1960 : 1331). In the original description of the only species, the periphery (termed venter in cephalopod terms) is rounded (Lintz & Lohr 1958 : 980). If this is a correct interpretation of slightly crushed material then *Elkoceras* differs from *Phanerotinus*. In a later correction, Lintz (1962 : 612) accepts that *Elkoceras* belongs to the Euomphalidae, including it as a synonym of '*Straparollus (Euomphalus)*'. Based on the figure and description of Lintz & Lohr (1958) we prefer to retain the genus in the Euomphalidae provisionally as a separate genus of uncertain affinities.

Phanerotinus cristatus (Phillips)

Figs 1-4

- 1836 *Euomphalus cristatus* Phillips : 225, 249; pl. 13, fig. 5.
 1843 *Euomphalus cristatus* Phillips; Morris : 144, 155.
 1843 *Phanerotinus cristatus* (Phillips) J. de C. Sowerby : pl. 624, fig. 1.
 1844 *Phanerotinus cristatus* (Phillips) J. de C. Sowerby : 30.
 1854 *Phanerotinus cristatus* Sow.; Morris : 267.
 1881 *Phanerotinus cristatus* (Phillips); de Koninck : 107.
 1915 *Phanerotinus cristatus* (Phillips); Cossman, 10 : 177.
 1941 *Phanerotinus cristatus* (Phillips); Knight : 239-40, fig. 19; pl. 70, figs 1-2.
 1960 *Phanerotinus cristatus* (Phillips); Knight *et al.* I : 194, fig. 109.6.

MATERIAL. Holotype: BM(NH) reg. no. G184 and counterpart from the William Gilbertson collection, presumed to be the holotype by Knight (1941 : 239). An entry in an MS entitled *A Catalogue of Mountain Limestone Fossils in the collection of Wm. Gilbertson . . .*, assumed to be by Gilbertson and of which the Palaeontology Library, BM(NH) holds a photographic copy, states on p. 14 against no. 269: 'E. cristatus, this unique specimen . . .'. This establishes that Knight's conclusion was correct and that G184 is the only known specimen in the Gilbertson collection.

2. BM(NH) reg. no. G72, purchased from the Executors of J. Tennant in September 1881; referred to by Knight (1941 : 239).

3, 4. Institute of Geological Science reg. nos. LZB 29 and LZB 34; collected by R. Dixon in November 1978.

At a late stage (June 1981) P. Doughty of the Ulster Museum, Belfast, informs us that they have two specimens of *Phanerotinus cristatus* in their collections. These were collected from



Fig. 1 *Phanerotinus cristatus* (Phillips), holotype. Basal view of steinkern which shows rounded end of body whorl septa, traces of growth lines and the peripheral spines. BM(NH) G184, $\times 0.9$; Carboniferous Limestone, ? Bolland, or Whitewell, Yorkshire; William Gilbertson collection, purchased 1841.

Athlone by Robert Young (1821–1917), a railway engineer, and presented to the Belfast Natural History and Philosophical Society. In K5119 a third of an outer whorl is preserved in matrix (diameter of shell 18–20 cm, plus spines 30 cm), and in K1665 there is half of a whorl with a diameter of 17 cm, but no spines. In thin sections from the matrix of K5119 John Wilson of the Ulster Museum has recently found large specimens of the foraminifer *Ammarchaediscus* (*Rectodiscus*) sp. These are normally indicative of a late Arundian age.

The specimen listed by Carrington (1865 : 49) from Wetton, Derbyshire as *Phanerotinus cristatus* is now in the Sheffield City Museum; upon examination it proved to be a fragment of the brachiopod *Pugnax*.

Stubblefield in Mitchell & Stubblefield (1941) identified possible examples of *Phanerotinus cristatus* in a fauna from the *Productus humerosus* Beds ($=C_2$) at Breedon-on-the-Hill, Leicestershire, but although this material should be in the IGS collections we have been unable to examine the specimens.

OCCURRENCE AND LOCALITY. J. de C. Sowerby recorded that the figured specimen (G184) was from 'Whittle' in Yorkshire, while Phillips had earlier given the locality as Bolland. It is now realized that Phillips used the locality Bolland in a much more restricted sense than Gilbertson. In the spring of 1835, Phillips had carried out an extensive geological survey of that district, whereas Gilbertson simply used the name for the broader district in which he



Fig. 2 *Phanerotinus cristatus* (Phillips). Basal view; the septa are visible as faint concave lines in the remnants of the early whorls at centre right; the inner carina is visible at lower right. IGS LZB 34, $\times 0.8$. ? Red Hill Oolite, Carboniferous Limestone, ? Arundian; Plumpton Quarries, near Ulverston, Cumbria (SD 3072 7848); found in wall by R. Dixon, November 1978.

collected. In discussing Bolland, Phillips (1836 : 20) mentioned both Whitewell and the Whitewell Inn and this is presumably the locality to which Sowerby referred. Phillips also commented that the limestone might be considered to form two oval exposures in the area, one centred on Slaidburn and the other on Chipping with Whitewell close to its boundary. Arbour (or Thornley) Quarry, near Chipping, Yorkshire has been suggested as the probable site for many of Gilbertson's specimens, but it is felt that they would all have come from quarries in the Clitheroe district (personal communication M. Mitchell, N. Riley, R. Grayson and C. H. C. Brunton), although this obviously does not apply to his activities on the Isle of Man.

The locality of Tennant's specimen (G72) has not been recorded, but in the catalogue of his collection Tennant (1858 : 64) records a specimen of *Phanerotinus cristatus* as coming from Ireland. However, the matrix of G72 would appear to be very similar to that of G184.

The two IGS specimens were found loose at different places in the extensive workings at Plumpton, near Ulverston, Cumbria. It has been suggested from a comparison of their lithologies that both specimens came from the Red Hill Oolite (which is a pelleted limestone,

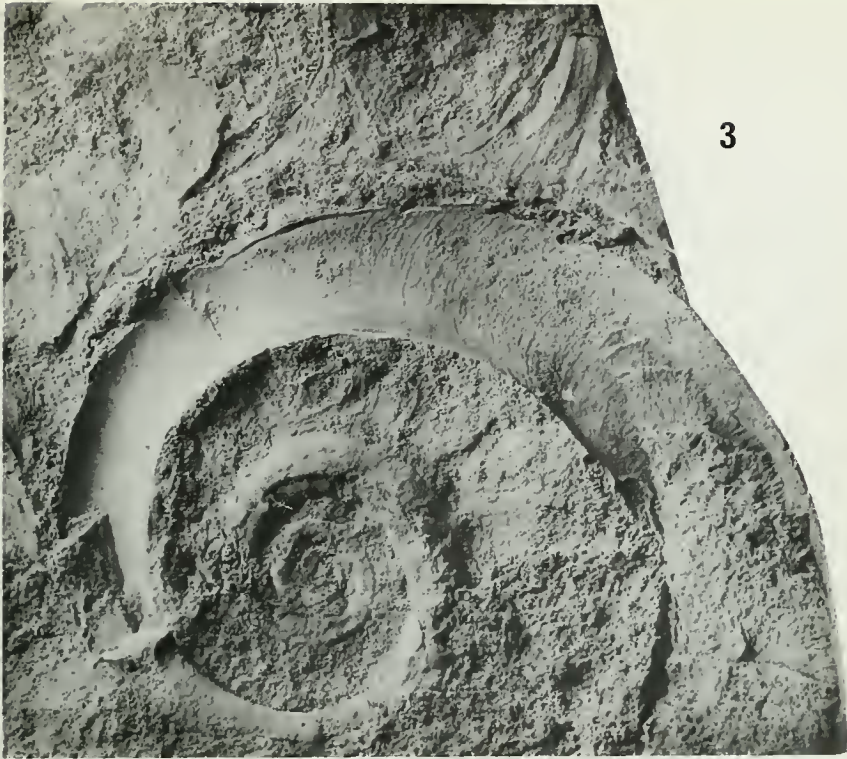


Fig. 3 *Phanerotinus cristatus* (Phillips). Latex mould of specimen shown in Fig. 4, showing impression of early whorls and a mould of the body whorl preserving the dorsal emargination and faint traces of its spines. BM(NH) G72, $\times 1.5$.

not an oolite) of early Arundian age (personal communication M. Mitchell). Rose & Dunham (1978 : 29, 161) mention that fossils are not common in the Red Hill Oolite, but small simple corals, e.g. *Koninckophyllum* cf. *praecursor* and *Palaosmilia purchisoni*, can generally be found together with specimens of the tabulate coral *Michelinia megastoma*; they also state that the fauna is typical of the C₂S₁ Zone. However, we are not entirely confident that the preservation of the originally larger shell (LZB 29) is identical to that of the other (LZB 34), which we understand was collected from a wall! The rock matrix of LZB 34 contains many crinoidal ossicles which do not occur in any of the other specimens.

DESCRIPTION. Large-size discoidal gastropods, with coiling interpreted as dextral, but with the majority of whorls showing a characteristic wide open coiling. (Although the early whorls are preserved it is not possible to discern their character accurately.) The early whorls are partitioned off by a transverse septum, or septa, with concave side forward. Four to five whorls are present in the more complete specimens.

Whorl cross-section subcircular but slightly asymmetrical, being rather wider than high and with the dorsal angulation closer to the inner margin. The upper and basal lips are sub-radial. The aperture is noticeably prosocline. A hollow spine-like extension of the outer apertural lip occurs in the lower third of the whorl circumference and produces a corona of large thorn-like extensions; a much smaller and shorter spine occurs at the same level on the inner lip of specimen G72 while in IGS LZB 34 the inner side of the whorl is relatively smooth for much of its length but has an irregular carina.



Fig. 4 *Phanerotinus cristatus* (Phillips). The dorsal emargination is preserved in an external mould of the early whorls. The growth lines on the base of the whorl and the peripheral spines of several whorls are also shown. Note that the spines are close to the inner margin of the succeeding whorl. BM(NH) G72, $\times 1.1$. Carboniferous Limestone, locality not recorded; James Tennant collection, purchased from his executors 1881.

The upper lip has a small V-shaped dorsal emargination, which bears short hollow spines directed towards the aperture; the prominent fine and evenly-spaced growth lines are opisthocyrte on either side of this 'selenizone', crossing the dorsal spine and extending progressively forward over the top of the peripheral spines, but turning sharply backwards on their lower surface. The spines are more frequent on the inner whorls than the later ones, but are much smaller. The presence of the spines markedly increases the diameter of the shell, which comparison of the following measurements, taken wherever preservation permitted, confirms.

	G 186	G 72	LZB 34	LZB 29
Diameter of steinkern	105 mm	97 mm	150 mm	152 mm
Diameter with spines	195 mm	160 mm	245 mm	—
Height of steinkern	—	22 mm	—	—
Width of steinkern	—	—	—	38 mm

DISCUSSION. The limited number of available specimens of this remarkable gastropod and their poor preservation have prevented a satisfactory interpretation of its biology. Yet, despite these drawbacks, earlier authors have assigned *Phanerotinus cristatus* to the Euomphalidae.

Its general shell morphology indicates such a relationship, for the presence of the upper whorl angulation and the regular series of opisthocyrt growth lines are characteristic of that family. The discovery of a slight V-shaped dorsal emargination coinciding with the angulation provides further confirmation of this classification; in common with all living Pleurotomariacea and Fissurellacea this feature would tend to divide the aperture. Such a slit accommodates the exhalant current and the dispersal of faeces from the closely situated anus, while dividing the mantle cavity into areas occupied by the right and left gills. The close similarity in shell morphology between many Euomphalacea and Pleurotomariacea leads to the conclusion that the majority of these gastropods also had a central dorsal anus and exhalant current, with symmetrically-paired gills on either side. Knight's (1941 : 239) description of the protective sheaths as open groove-like canals extending from the outer lip is correct, but his suggestion that these were excurrent is surely mistaken. The implications of his interpretation would be that the post-torsional right gill was hypertrophied; no such mollusc has ever been described. We hold the opposite view that this current could only have been inhalant, and we feel that such an interpretation is consistent with the bizarre nature of the shell of *Phanerotinus*.

As there is no apparent change in the shell geometry during its ontogeny, *Phanerotinus* must be regarded as open-coiled throughout most of its life. However, this conclusion is based on the poorly-preserved examples listed above, which give no clear evidence of the early whorls. Yochelson (1971 : 237) gives several factors as being responsible for open coiling, but indicates that these are not of a different nature from the logarithmic factors involved in normal coiling. In the case of *Phanerotinus*, it is the increase in the factor D (Raup 1966, Vermeij 1971 : 16), i.e. the distance of each whorl from the axis, which is solely responsible. This increase is due to slightly varied rates of shell deposition on either side of the whorl. The inner side of the shell grows comparatively faster than in most other gastropods and this results in bringing it further away from the axis.

Consideration of the probable advantage of open coiling, together with the presence of spines, indicates:

1. A sedentary/sessile mode of life and filter feeding. Open coiling would be quite unsuitable for regular locomotion and so would rule out an active benthonic existence, a point made by Yochelson (1971 : 240) when he described *Nevadaspira*.
2. The lengthy thorn-like spine on the outer whorl margin extends the area of the aperture and thus improves the efficiency of the mantle current and provides optimum conditions for filter feeding.
3. The extension of the relatively smooth, flat bottom of the shell provided by these spines would increase the area in contact with the bottom; on soft sediments this might prevent sinking by spreading the load. We also believe that the spines would contribute to stability of the shell by preventing it from being overturned and ensuring that it maintained its position on the sea floor.
4. The spines could have afforded protection to the gastropod from predators such as fish, but we believe that this is less likely.

Phanerotinus resembles the open-coiled Ordovician genus *Ecculiomphalus* Portlock (Knight 1941 : pl. 71, figs 3a-c) and also *Lytospira* Koken, but lacks the deep V-shaped sinus which these genera usually have. We have examined the type material of *Ecculiomphalus*; in this genus there is a continuous peripheral flange, in contrast to the peripheral spines of *Phanerotinus* (Fig. 5); it should be pointed out that the figure in the *Treatise* (Knight *et al.* 1960 : fig. 107.5a-b) actually shows *Eccyliopectus*. Superficially, the general ornament of *Phanerotinus* resembles that of the north European Silurian genus *Poleumita* Clarke & Ruedemann, but this genus does not have peripheral spines. The similar open coiling occurring in the Devonian and Carboniferous genus *Serpulospira* Cossmann would seem to be convergence, for its virtually smooth ornament suggests to us that the two genera are not closely related. We suspect that in *Phanerotinus* we are dealing with a rather rare taxon, or at least one that only occurred in a restricted environment and whose closer relatives remain to be discovered.

Characteristics and relationships of the Euomphalacea

Shell Structure

Knowledge of the shell structure of the Euomphalacea is based upon evidence found in a very small proportion of the taxa normally placed in this superfamily. Knight (1934) described the essentially two-layered nature of the shell as a prismatic outer layer (of unspecified mineralogy) and an inner layer which he thought might have been nacre. He later revised this opinion, for in co-operation with the other *Treatise* authors (1960 : 1189) he described the Euomphalacea as having 'shell wall relatively thick, with external prismatic layer of calcite which may be pigmented and internal layer of aragonite which is lamellar and not nacreous'. His use of 'lamellar' apparently refers to the growth of laminae of the inner layer.

Yochelson, White & Gordon (1967), in their x-ray diffraction analysis of the mollusca from the Pennsylvanian Kendrick Shale, showed that *Amphiscapha* had a calcite outer layer and an aragonitic inner layer. It is possible that this material may have been recrystallized to a certain extent, with unstable aragonite changing to calcite, as minor amounts of calcite were found in the associated bivalves '*Yoldia*' and '*Parallelodon*' which would have originally been aragonitic. We have, however, been able to confirm their findings in two new examples. The twofold shell structure is clearly visible in polished and etched sections of *Amphiscapha subrugosa* (Meek & Worthen), BM(NH) PG5089, from the Cisco Formation collected at Fort Graham, Texas, although both layers have suffered from some recrystallization. The ghosts of original shell structures are commonly preserved in the associated molluscan fauna. These have been described by McClintock (1967), Batten (1972) and Morris (1979), and have also been observed by us in both Crassatellacean bivalves and Subulitacean gastropods. In at least one example, *Pseudoconocardium lanterna* (Branson), x-ray powder diffraction analysis has shown that they are now preserved as calcite (A. Hall personal communication). The ghost structures include nacre and crossed-lamellar structure, both of which must have originally been aragonitic as they are always formed of aragonite today.

In *Amphiscapha*, the outer calcite layer is preserved as a deep grey pellucid layer, while the inner recrystallized and originally aragonitic layer is preserved as a buff or orange-buff opaque layer, in which radiating cross lamellae are clearly visible on the etched sections of better-preserved specimens.

The outer calcitic layer has, clearly preserved, growth laminae and small-scale radiating prisms that fan out (Fig. 11, p. 209) at the anal emargination and the outer carina. Its calcitic layer is not composed of large-scale hexagonal prisms as in pteroid bivalves (Taylor *et al.* 1969), but is more like the outer layer of *Chama pellucida* (Kennedy, Taylor & Morris 1970), although the large blocky units they describe have not been observed. Within the Gastropoda, in addition to occurring in the Patellacea, Neritacea and Platyceratacea, calcitic outer layers have been recorded for certain buccinaceans and muricaceans.

The inner layer has well-preserved growth laminae with radiating crossed lamellae normal to the outer shell interface in transverse section and approximately aligned with the whorl in tangential section. These are typical gastropod crossed lamellae and there is every reason to believe that the structure was originally aragonite. We have not been able to discover the shell structure of the septa, or any additional inner layer that might be confluent with them.

A specimen of *Euomphalus* sp., BM(NH) PG5088 from the Upper Pennsylvanian Buckhorn Asphalt of South Oklahoma, also shows a similar outer layer of calcite. The inner layer of this species was presumably aragonitic for it was not preserved in the same way and has largely been destroyed. The occurrence of well-preserved nacre and crossed lamellar structures, in associated specimens of cephalopods and neritaceans respectively, may reflect that the single euomphalid specimen is poorly preserved.

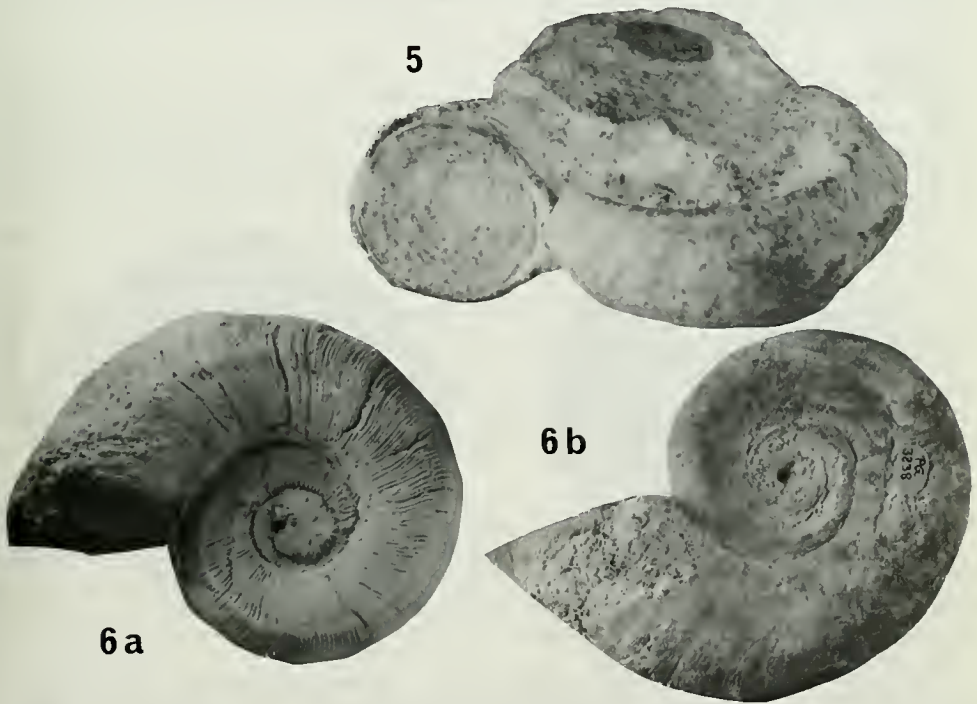
The presence of an outer calcitic layer in both *Amphiscapha* and *Euomphalus* suggests, but does not prove, that this structure was widespread in the Euomphalidae. At present, we adhere to the normally-accepted view of molluscan shell structures, which interprets the

aragonitic nacreoprismatic shell as the primitive type of calcareous shell of the conchiferan Mollusca (Taylor 1973). This type commonly occurs in cephalopods, archaeogastropods and different groups of bivalves and at least one rostroconch. It would seem that the calcitic outer layer of the Euomphalidae is a character developed separately from other gastropods.

Opercula of the Euomphalacea

It is reasonable to assume that the presence of an operculum is primitive, that virtually every known Palaeozoic gastropod had an operculum, and that almost all these animals retained them throughout life (Yochelson & Linsley 1972). Remarkably few opercula are preserved, because it is only rarely that their organic material served as a matrix for calcification; fossilization normally occurs only when the operculum has been calcified as in some members of the Trochacea and among the Neritacea. Linsley & Yochelson (1973: 17) argued for a non-calcified operculum in those members of the Euomphalacea that have adherent shell fragments.

The operculum, found in place, of the Australian Devonian, seemingly left-handed, *Euomphalus northi* (Etheridge) described by Yochelson & Linsley (1972) is multispiral or finely concentric on its outer surface and was apparently originally calcified (Fig. 5). Its growth increments at the periphery may be traced inwards. These follow the outer edge and then turn to form the smooth inner surface, which resembles a flattened ring-doughnut with



Figs 5, 6 *Euomphalus northi* (Etheridge, jr). This species is considered to be coiled sinistrally because the angulation which is present is assumed to be on the dorsal surface. Fig. 5, oblique apertural view with operculum in place; BM(NH) PG3649, $\times 1.6$. Fig. 6, BM(NH) PG3838, $\times 0.9$; a, dorsal view; b, basal view, showing the typical relatively smoother surface. Both specimens from the Lilydale Limestone, Lower Devonian, Yeringian; Cave Hill Quarries, Lilydale, Victoria, Australia; C. T. Trechmann collection, bequeathed 1964.

a flat disc-shaped surface filling the central hole and forming a slight depression. Its general form is comparable with that of the opercula of Trochidae and Pleurotomariidae, but this may only be the result of its similarity in fitting a circular aperture. The outer surface resembles that of some species of *Oriostoma* (Lindström 1884), but the inner surfaces of opercula belonging to the Oriostomatidae do not have the same radial symmetry.

The multispiral or concentric operculum of *E. northi* is in sharp contrast to the paucispiral operculum found in *Maclurites*, which leads us to suspect that they are not closely related. This evidence cannot, however, be taken as proof because the calcified paucispiral operculum of the Turbinidae (Trochacea) has apparently evolved from the multispiral uncalcified operculum possessed by their close relatives the Trochidae and Pleurotomariidae.

The growth increments in the euomphalid operculum are separated by narrow concentric slits when viewed from the outer surface; examination of the broken outer edge shows that some of these follow each increment to its inner surface. This suggests that each apparent calcereous layer was separated by a slightly narrower organic layer. The purpose of the central depressed area on the inner surface of the operculum is not clear. Two possible explanations are that the area either marks the position of attachment of the foot, or that it represents the juvenile stage when the operculum was much thinner.

The opercula of other genera of Euomphalacea are now known, e.g. *Polhemia* and *Oreospira* (Knight *et al.* 1960 : 1189), *Ceratopea* (Yochelson & Wise 1972) and *Helicotoma* (Yochelson 1966*a*). These are quite unlike that of *Euomphalus* and lead us to keep these genera in a separate family.

Septation

Yochelson (1966*b*, 1971 : 238–9) and Linsley & Yochelson (1973 : 21) have discussed the occurrence and preservation of septation in the Euomphalacea and in doing so emphasized the inadequacy of existing knowledge. The steinkerns of three specimens of *Phanerotinus* show a very marked rounded end, indicating the presence of the septum at the end of the living chamber. In IGS LZB 34, there are indications of at least five septa in a whorl length of 5 cm in the earlier whorls (Fig. 2). Unfortunately, the specimens are not sufficiently well preserved to permit the frequency of septa to be related to the frequency of spines.

We suggest that septation allowed the gastropod to vacate early-formed, narrow whorl space and occasionally to lose its earlier whorls without undue disturbance. Early whorls are frequently absent in a number of euomphalid specimens. This view is offered as an alternative to those of Yochelson (1971), who postulated that the septa were formed to strengthen the shell, or as a consequence of the physiological requirement to remove and utilize calcium carbonate caused by the sessile habit, or were the result of shortening the body apparently as an adaptation to a sessile mode of life (Linsley & Yochelson 1973 : 21).

Open coiling

Within the Euomphalacea the open-coiled form is relatively common, but is far outnumbered by conjoined coiled forms, both in numbers of species and of individuals. However, both types occur early in the history of the family, e.g. during the Lower Ordovician, and we cannot deduce from the euomphalaceans alone which is the more primitive form. It is the normally accepted view that a closely or conjoined coiled shell is a primitive feature of the Gastropoda.

Yochelson (1971 : 236) defined gastropods which lack conjoined whorls as 'open-coiled' and used the term 'uncoiled' for taxa resembling *Vermetus* which have profound deviations in shape caused by changes in life habit. This definition of 'uncoiled' would seem to require clarification and its use should best be confined to taxa lacking regular spiral form. Peel (1975 : 214) discussed open-coiled gastropods and divided them into four, what he described as 'loose morphological', categories, though he apparently attached no real significance to any one of them: he did not specify into which category he placed *Phanerotinus*. Both

authors followed Linsley (1968) in recognizing that variation in shape within open-coiled species stretched beyond the normal limits accepted for gastropods.

In common with Yochelson (1971) and Peel (1975), we interpret the widely phaneromphalous, discoidal and open-coiled nature of most Euomphalaceans as a reflection of a relatively sessile habit and agree with them that this is probably an adaptation for filter feeding. Such a conclusion is based on a comparison with the filter-feeding Vermetidae, of which widely disjunct coiling is also a feature. They are usually considered to be related to the tightly coiled but tall Turritellidae, which are also filter feeders. However, Linsley & Yochelson's living examples the Xenophoridae, although mainly sessile, are not open-coiled and are thought to be algal grazers. The Upper Palaeozoic Omphalotrochidae have relinquished the discoidal phaneromphalous form, but whether or not these were also filter feeders is more uncertain.

Orientation of the Euomphalacea

Both the Ophiletidae and Euomphalidae include open-coiled forms that are most satisfactorily interpreted as filter feeders. Acceptance of this may imply that the discoidal and conjoined taxa of both groups were also filter feeders, or at least largely sessile. If the Ophiletidae are correctly interpreted as right-handed and normally torted, then the position of the anal emargination which lies at the periphery, either at the mid-whorl or dorsally, suggests that the animal was orientated quite differently from any of the Euomphalidae. In those Ophiletidae where the emargination is in the mid-whorl position, the dorsoventral axis of the mantle cavity and the lower part of the animal would be at right angles to the axis of coiling. Although this is the conventional orientation of prosobranchs, it would make locomotion extremely difficult for an animal with a horizontally held discoidal shell, and would thus indicate a sessile habit. The euomphalid orientation, where the dorsoventral axis is apparently parallel to the coiling axis, may have developed from the ophiletid orientation by turning through 90° to facilitate occasional locomotion.

Having recognized a dorsal anal emargination in the Euomphalidae (Figs 9–10, p. 208)



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Fig. 7 *Poleumita discors* (J. Sowerby); shows ornament of short spines on dorsal emargination (= sinus) and its procline growth lines. BM(NH) 73893, $\times 1$; Wenlock Limestone, Silurian; Bethal Edge, near Much Wenlock, Shropshire; purchased from S. Allport, March 1873.

Fig. 8 *Euomphalus pentangulatus* J. de C. Sowerby; shows typical growth lines, its smooth shell and the dorsal angulation of euomphalaceans. BM(NH) 43619, $\times 1$; Carboniferous Limestone, near Preston, Lancs.; originally belonging to Gilbertson collection but part of Sowerby collection, purchased January, 1861.

and by using its presence axiomatically, we can recognize a large number of right-handed taxa in the Euomphalacea and a much smaller number of left-handed taxa. The commonly accepted interpretation of euomphalid orientation, which we in fact follow, is further supported by the nature of the surface ornament. In the Silurian genus *Poleumita* (Fig. 7) the conventionally-interpreted upper surface is much more ornate than the virtually featureless lower surface. To a lesser extent, this situation prevails in the examples of *Phanerotinus* described above. The classification of the Euomphalacea below distinguishes left-handed taxa. However, left-handed forms occur in some taxa which are generally right-handed; e.g. within the genus *Euomphalus* itself, *Euomphalus northi* (Etheridge) from the Lower Devonian of Australia is a left-handed form (Fig. 5, p. 203).

Morphological similarities and relationships

The discoidal form of the Euomphalidae occurs in three other groups represented in the Ordovician, the Helicotomidae, the Trochonematacea and the Pseudophoracea. All three have a radially-situated prosocline aperture, but only the Helicotomidae have an anal emargination comparable to that of the Euomphalidae. *Helicotoma* is intermediate in orientation between *Ophiletina* and early euomphalids and is almost certainly correctly placed in the same superfamily. The trochiform shape and the lateral emargination of the Pseudophoracea suggest an inhalent current at the base of the periphery and the existence of only one gill. The similarity of form between the Trochonematidae and some early Palaeozoic Pleurotomariacea led Knight *et al.* (1960) to suggest that this group may also have had paired ctenidia, but the evidence here seems to be equivocal. The similar discoidal shape of the shell in all these groups may indicate a close common ancestry in pre-Ordovician times.

We are struck by the similarity of *Sinuopea* (Pleurotomariacea) and *Holopea* (Platyceatacea). The former has the primitive shell form of the Pleurotomariacea, turbiniform with a marked anal emargination in the form of a broad sinus in the outer lip, while *Holopea*, although lacking the sinus and anterior emargination, has the same overall turbiniform shape. Together with the many characters mentioned by Fretter & Graham (1962 : 612–3) as shared by the Pleurotomariacea and Trochacea, we feel that this is indicative of the primitive form likely to be shown by the ancestor of the Pleurotomariacea, Trochacea and Neritacea, which is inferred to have had paired ctenidia in addition to paired kidneys. It follows that the commonly-held view (Yonge & Thompson 1976 : 50) that left and right paired ctenidia are a primitive feature of the gastropods is accepted; symmetrically-paired gills occur in most other living Mollusca.

But we do not believe that an anal emargination of the shell and mantle is a feature of the earliest gastropods: in other words we do not consider that it is a synapomorphic character of the whole class. In our view it arises convergently in the Mollusca, particularly in some gastropods and Monoplacophora because of the advantage of placing the anus in the exhalent current. It is suggested here that the anal emargination has evolved separately in the Euomphalacea and possibly on more than one occasion. This would not be particularly unusual as, for example, this feature appears to have arisen at least twice in the Bellerophonacea, in which the animal is regarded as untorted and best classified with the Monoplacophora (Morris & Cocks, in prep). It is also considered that the slit may have arisen on more than one occasion in the group currently classified as Pleurotomariacea. Moreover, the posterior exhalent and anal sinus has clearly developed entirely independently in the neogastropod family Turridae.

The Euomphalacea are an early, but distinct, group of the Archaeogastropoda, which apparently did not survive beyond the earliest Mesozoic. What little is known of the shell structure of *Euomphalus* and *Amphiscapha* supports the view expressed by Sohl (1960) that Mesozoic genera ascribed to the Euomphalidae by both Wenz (1938) and Knight *et al.* (1960) are misplaced.

Two genera from the Albian, *Discohelix* and an astraeform species tentatively regarded as

Jurassiphorus, are included with the genera *Vivianella*, *Paraviviana*, *Colpomphalus*, *Platybasis* and *Nummocalcar* in a group of nacreo-prismatic shells of typical aragonitic structure within the Trochina. *Weeksia* has an entirely crossed lamellar shell with a multi-whorled hyperstrophic protoconch and appears to be an Architectonicacean. There is some uncertainty about the Triassic genera *Woehrmannia*, *Anisostoma* and *Amphitomaria*, but the Jurassic *Coelodiscus* and the Upper Cretaceous *Condonella* are certainly not correctly included in the Euomphalacea and their true taxonomic position must remain doubtful.

Classification of the Euomphalacea

As a result of our studies of euomphalacean gastropods, we have provisionally re-arranged the genera belonging to this superfamily and incorporated others that we think were wrongly assigned elsewhere. (For taxa references, see Knight *et al.*, 1960).

Subclass **PROSOBRANCHIA** Milne-Edwards, 1848

Order **ARCHAEOGASTROPODA** Thiele, 1925

? Suborder **PLEUROTOMARIINA** Cox & Knight, 1960

The Euomphalacea are tentatively removed from the Macluritina, and placed in the Pleurotomariina, as they at least share the assumed primitive character of paired ctenidia. It is by no means certain that they share any character with the Macluritacea apart from the coiled shell.

Superfamily **EUOMPHALACEA** de Koninck, 1881

Mainly discoidal phaneromphalous shells with some later trochiform taxa; often with dorsal emargination suggestive of an exhalent current close to the anus and separating paired gills; emargination varying from peripheral to apical position on the aperture; shell septa commonly present; calcareous opercula preserved in several taxa. Shell composition of calcite and aragonite occurs in the Euomphalidae. A number of open-coiled taxa known.

Family **OPHILETIDAE** Knight, 1956

[*nom. transl.* herein, *ex* Ophiletinae Knight, 1956]

Dorsal emargination in the form of a broad and deep V-shaped sinus; shell with little ornament; horn- or wedge-shaped opercula present in *Ceratopea*. We recognize four informal groups:

1. Group with sinus in peripheral position. *Schizopea* Butts, 1926 (U. Camb. – L. Ord.), *Dirhachopea* Ulrich & Bridge, 1931 (U. Camb. – L. Ord.), *Ceratopea* Ulrich, 1911 (L. Ord.), ? *Pararaphistoma* Vostokova, 1955 (Ord.), *Ophileta* Vanuxen, 1842 (L. Ord.), *Ozarkispira* Walcott, 1924 (L. Ord.), *Calaurops* Whitfield, 1866 (L. Ord.).
2. Group with sinus at top of aperture when axis of coiling is positioned vertically. *Barnesella* Bridge & Cloud, 1947 (L. Ord.), *Lecanospira* Butts, 1926 (L. Ord.), *Lesueurilla* Koken, 1898 (Ord.).
3. Group with the same characters as 2 but open-coiled. *Lytospira* Koken, 1896 (L. Ord. – M. Sil.), *Ecculiomphalus* Portlock, 1844 (U. Ord.), *Mastigophora* La Rocque, 1949 (Dev.).
4. Group similar to 3 but with addition of a selenizone. *Ophilitina* Ulrich & Schofield, 1897 (M. Ord.), *Odontomaria* Roemer, 1876 (M. Dev.).

Family **HELICOTOMIDAE** Wenz, 1938

Dorsal emargination shallower than in the Ophiletidae, occurring at top of outer lip position and often carinate, with a notch or short slit, sometimes developing into a selenizone; spire

slightly elevated. Calcareous operculum with few whorls in *Helicotoma*, but described as wedge-shaped in *Polhemia* and *Orospira*. *Eccylopterus* is open coiled.

Lophonema Ulrich in Perdue & Miser, 1916 (L. Ord.), ? = *Polhemia* Cullison, 1944 (L. Ord.), ? = *Orospira* Butt, 1926 (L. Ord.); *Helicotoma* Salter, 1859 (L.-U. Ord.); *Eccylopterus* Remelé, 1888 (Sil.).

Family EUOMPHALIDAE de Koninck, 1881

Round-whorled with emargination not deep and approximately in the central apical position of the whorl, but secondarily peripheral in later forms. Occasionally ornamented with spines, or scale-like projections; conjoined and open-coiled forms; left-handed taxa not uncommon. Shell of *Euomphalus* and *Amphiscapha* composed of an outer layer of calcite prisms and an inner layer of cross-lamellar aragonite. Calcified operculum present in one species of *Euomphalus*. We recognize three informal groups:

1. Group with conjoined or nearly joined whorls. Some Devonian species of *Euomphalus* and *Straparollus* bear adherent peripheral shell fragments; the name *Philoxene* Kayser (1889) has been used for one of these species (Linsley & Yochelson 1973:19). *Macluritella* Kirk, 1927 (L. Ord.), *Euomphalopsis* Ulrich & Bridge, 1931 (L. Ord.), *Poleumita* Clarke & Ruedemann, 1903 (Sil.), *Centrifugus* Bronn, 1834 (U. Sil.), *Sinutropis* Perner, 1903 (U. Sil.), *Euomphalus* J. Sow., 1814 (Sil.-M. Perm), *Straparollus* Montfort, 1810 (Carb.), *Philoxene* Kayser, 1889 (Dev.), *Leptomphalus* Yochelson, 1956 (Carb.-Perm.), *Omphalocirrus* Ryckholt, 1860 (Dev.) (left-handed), *Pleuronotus* Hall, 1879 (Dev.).
2. Group with open-whorled form, some bearing large spines; some others with adherent shell fragments. *Serpulospira* Cossmann, 1916 (Dev.-U. Carb.), ? *Nevadispira* Yochelson, 1971 (U. Dev.), *Phanerotinus* J. de C. Sowerby, 1843 (L. Carb.) *Sinistrospira* Jhoweri, 1969 (Dev.), ? *Elkoceras* Lintz & Lohr, 1958 (L. Carb.).
3. Late Palaeozoic - ? Mesozoic group with dorsal emargination secondarily moved laterally towards dorsal edge of outer lip. *Amphiscapha* Knight, 1942 (U. Carb.-Perm.), *Cylictoscapha* Yochelson, 1956 (U. Carb.-Perm.), ? *Planotectus* Yochelson, 1946 (M. Perm), ? *Woehrmannia*, Böhm, 1895 (M.-U. Trias), ? *Amphitomaria* Koken, 1897 (M. Trias), ? *Anisostoma* Koken, 1889 (M.-U. Trias).



Fig. 9 *Straparollus* sp.; shell shows growth lines and the selenizone at the dorsal emargination on the outer whorl. BM(NH) 64756, $\times 1$; Carboniferous Limestone, Visé, Belgium; purchased from L. G. de Koninck, 1868.

Fig. 10 *Straparollus* aff. *acutus* (J. Sowerby); top surface showing dorsal sinus and growth lines. BM(NH) G41144, $\times 1.6$; St Doolagh, Co. Dublin, Ireland; Carboniferous, Visean Zone D₂; Wheelton Hind collection, purchased 1921.

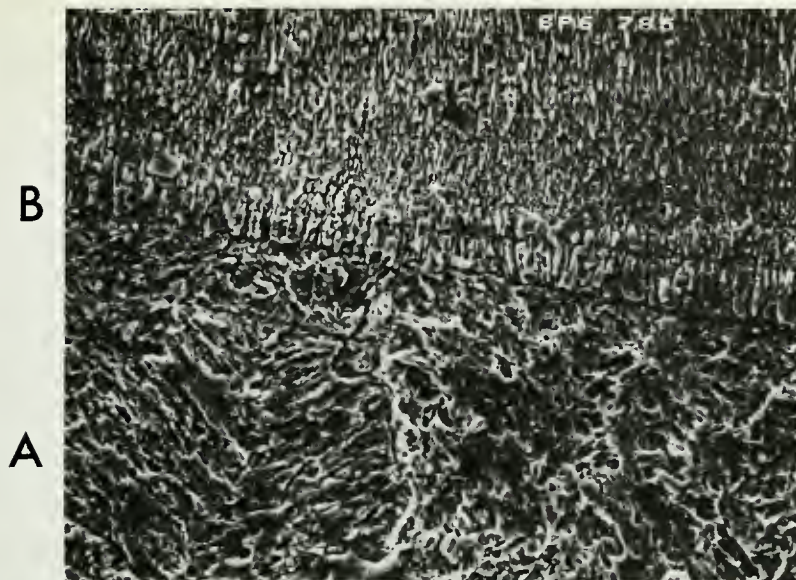


Fig. 11 Shell structure of *Amphiscapha subrugosa* (Meek & Worthen). Gold-coated polished and etched surface cut radially through outer whorl. Scanning electron micrograph, approx. $\times 400$. A, Inner shell layer composed of a single set of parallel-sided first order lamellae with their short axes concentric with the shell surface. They are parallel to the aperture and formed of fine laths forming a herringbone pattern resembling polysynthetic twinning. These are interpreted as being originally aragonitic. B, Outer layer of radially-orientated fine prisms, interpreted as originally being calcitic. Upper Pennsylvanian, Texas, BM(NH) PG5089.

Family OMPHALOTROCHIDAE Knight, 1925

Trochiform euomphalaceans with anal emargination dorsal; central in *Discotropis*, but apparently in a broad shallow sinus on the whorl side in other genera. Operculum unknown.

? *Micromphalus* Knight, 1945 (M. Dev. – L. Carb.), *Orecopta* Knight, 1945 (Dev.), *Omphalotrochus* Meek, 1844 (U. Carb. – Perm.), *Discotropis* Yochelson, 1956 (U. Carb. – Perm.), *Babylonites* Yochelson, 1956 (Perm.), *Diploconula* Yochelson, 1956 (Perm.).

Summary of conclusions

Phanerotinus J. de C. Sowerby, 1844 has the typical characters shown by members of the Euomphalidae including what is interpreted as a dorsal anal emargination. The evidence indicates that the Euomphalidae may all have been filter feeders with two gills. As an adaptation for sessile living with a discoidal shell, the Euomphalidae are considered to have undergone 180° torsion in the normal anticlockwise direction and then rotated the mantle cavity with the lower part of the body clockwise through 90° within the shell aperture.

Some Euomphalidae are shown to have had a two-layered shell with an inner layer of crossed lamellar structure, thought to have been aragonitic originally, and an outer layer of fine prisms, thought to have been calcitic originally.

We are not convinced that there is a close relationship between the Euomphalacea and the

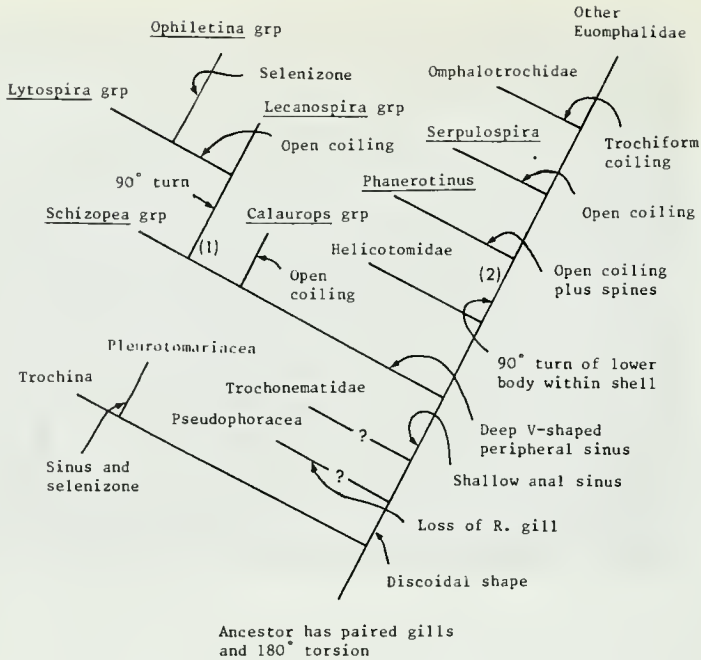


Fig. 12 Tentative outline of the phylogeny of the Euomphalacea with some synapomorphies. In this arrangement the 90° turn, additional to 180° torsion, takes place at points (1) and (2). The position of the Oriostomatacea is uncertain.

Macluritacea, but recognize that the Euomphalacea share some characters with the Pleurotomariacea although these may all be primitive gastropod characters. An initial radiation of the Euomphalacea seems to have taken place before the Ordovician and we suspect that other discoidal superfamilies, e.g. the Trochonematacea and the Pseudophoracea, may share close common ancestry with them; these views are summarized in an evolutionary diagram (Fig. 12).

A revised classification is proposed and this is essentially based on the nature of the aperture, which is considered to be related to the orientation of the mantle cavity within the shell.

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